

Biotic interactions may overrule direct climate effects on spring phytoplankton dynamics

URSULA GAEDKE*, MIRIAM RUHENSTROTH-BAUER*, INA WIEGAND*,
KATRIN TIROK*, NICOLE ABERLE†, PETRA BREITHAUPT‡, KATHRIN LENGFELLNER‡,
JULIA WOHLERS‡ and ULRICH SOMMER‡

*Institute for Biochemistry and Biology, University of Potsdam, Am Neuen Palais 10, D-14469 Potsdam, Germany, †Biologische Anstalt Helgoland, Alfred-Wegener Institute for Polar and Marine Research, Kurpromenade, D-27498 Helgoland, Germany,

‡Leibniz Institute of Marine Sciences IFM-GEOMAR (at Kiel University), Düsternbrooker Weg 20, D-24105 Kiel, Germany

Abstract

To improve our mechanistic understanding and predictive capacities with respect to climate change effects on the spring phytoplankton bloom in temperate marine systems, we used a process-driven dynamical model to disentangle the impact of potentially relevant factors which are often correlated in the field. The model was based on comprehensive indoor mesocosm experiments run at four temperature and three light regimes. It was driven by time-series of water temperature and irradiance, considered edible and less edible phytoplankton separately, and accounted for density-dependent grazing losses. It successfully reproduced the observed dynamics of well edible phytoplankton in the different temperature and light treatments. Four major factors influenced spring phytoplankton dynamics: temperature, light (cloudiness), grazing, and the success of overwintering phyto- and zooplankton providing the starting biomasses for spring growth. Our study predicts that increasing cloudiness as anticipated for warmer winters for the Baltic Sea region will retard phytoplankton net growth and reduce peak heights. Light had a strong direct effect in contrast to temperature. However, edible phytoplankton was indirectly strongly temperature-sensitive via grazing which was already important in early spring at moderately high algal biomasses and counter-intuitively provoked lower and later algal peaks at higher temperatures. Initial phyto- and zooplankton composition and biomass also had a strong effect on spring algal dynamics indicating a memory effect via the broadly under-sampled overwintering plankton community. Unexpectedly, increased initial phytoplankton biomass did not necessarily lead to earlier or higher spring blooms since the effect was counteracted by subsequently enhanced grazing. Increasing temperature will likely exhibit complex indirect effects via changes in overwintering phytoplankton and grazer biomasses and current grazing pressure. Additionally, effects on the phytoplankton composition due to the species-specific susceptibility to grazing are expected. Hence, we need to consider not only direct but also indirect effects, e.g. biotic interactions, when addressing climate change impacts.

Keywords: bottom-up, climate change, lakes, light, plankton, predictions, scenarios, shallow marine systems, simulation model, top-down

Received 19 March 2009; revised version received 8 May 2009 and accepted 27 May 2009

Introduction

Overwhelming evidence is accumulating that the earth's ecosystems respond to global climate change (Walther *et al.*, 2002). So far, most studies have focused

on temperature or climate indices (e.g. the NAO) and results were generally in accordance with expectations derived from first principals, e.g. pole-ward extensions of biogeographic species ranges and an earlier onset of biological spring events (flowering of tree species, bird migrations, nesting, etc., e.g. Cleland *et al.*, 2007). While the effects of a changing climate are well-documented for terrestrial systems there is still a lack of knowledge

Correspondence: Ursula Gaedke, tel. + 49 331 977 1900, fax + 49 331 977 1948, e-mail: Gaedke@uni-potsdam.de

on how climate change will affect aquatic biota. There is some evidence for latitudinal shifts in species distribution (Edwards *et al.*, 2002; Walther *et al.*, 2002) and for shifts in the timing of phytoplankton spring blooms which is one of the dominant features in the seasonal growth patterns of phytoplankton in temperate and cold oceans and lakes providing the energy and matter base for zooplankton and fish production (Weyhenmeyer *et al.*, 1999; Straile & Adrian, 2000; Gerten & Adrian, 2001; Weyhenmeyer, 2001; Edwards *et al.*, 2002; Stenseth *et al.*, 2002; Wiltshire & Manly, 2004). However, in addition to temperature spring phytoplankton growth may also be influenced by light, and only few pelagic studies have addressed the impact of climate change on biotic interactions such as predator–prey relationships so far (e.g. Wiltshire *et al.*, 2008 and citations therein) although trophic interactions are known to have substantial consequences for the functioning of pelagic ecosystems.

The underwater light climate experienced by the phytoplankton which depends on the incoming radiation, vertical mixing intensity and depth, and attenuation, plays a decisive role for the onset of the phytoplankton net growth following Sverdrup's (1953) critical depth hypothesis. It provided a theoretical framework for a mechanistic explanation where the onset of thermal stratification in spring seas acts as a switch from insufficient light to light sufficiency, because phytoplankton circulating through a shallow surface layer receive more light than phytoplankton circulating through a deep water column (Riley, 1957). This close coupling of the seasonal temperature (via stratification) and light regime does not exist in shallow systems where either the sea floor (e.g. German Bight, North Sea; many shallow lakes) or a halocline (e.g. Baltic Sea) restricts vertical circulation during winter.

While most studies reported an earlier onset of the spring bloom in warmer years, the opposite trend was found in the Helgoland Roads (North Sea) time series which was attributed to biotic interactions (Wiltshire & Manly, 2004). It was hypothesized that enhanced grazing by overwintering zooplankton during warmer winters should retard the spring bloom not only as a result of increased copepod densities but also due to higher grazing rates and an earlier timing of copepods in spring (Wiltshire *et al.*, 2008). Climatic conditions affect the quantity and composition of the plankton communities which successfully overwinter and provide the inoculum for the spring development. As phyto- and zooplankton respond differently to altered winter conditions, the initial relative and absolute phyto- and zooplankton biomasses and the timing of the algal spring bloom varies among years (Fransz *et al.*, 1991; Turner *et al.*, 2006; Wiltshire *et al.*, 2008). This suggests

that the response of the spring bloom to global warming cannot be understood without disentangling the factors temperature, light, grazing, and overwintering biomass, i.e. abiotic and biotic processes have to be considered in concert.

Experiments are the usual tool to separate the influence of factors usually correlated with each other in the field. Moreover, they provide the opportunity of exceeding the present day range of climatic variability and extend the scope to the more pessimistic scenarios of global change. However, experiments at the appropriate scale (ca. 1 m³ of water volume is requested for repeated sampling of zooplankton without disturbing the experiment) are operationally limited by the number of feasible experimental units in a fully controlled environment. This prevents a full factorial combination of all factors at sufficient replication and grading of the factor intensities. Combining experimental approaches with mathematical modeling therefore provides a way out of the dilemma since models enable to study an almost unlimited number of treatment combinations while the experiments can be used to calibrate and validate the model.

In this article, we use indoor mesocosm experiments with natural plankton communities from the Kiel Bight, Baltic Sea, Germany (Sommer *et al.*, 2007) as experimental component. Plankton communities were subject to four temperature regimes, the lowest one conforming to the 1993–2002 average of local sea surface temperatures, while the other ones were elevated by 2, 4, and 6 °C, in order to mimic moderate to drastic climate change scenarios (IPCC, 2007). While temperature regimes were uniform between the three experimental runs conducted in three subsequent years, the natural solar surface irradiances were reduced to 16%, 32% and 64% to mimic differences in cloudiness and underwater light attenuation. Hence, light regimes and inevitably also the initial biomass and composition of phyto- and zooplankton differed between the 3 years which implies that their effects cannot be disentangled by mere observation of the data. Analyzing the impact of light intensity was motivated by findings of increasing cloudiness or atmospheric water vapor content during warmer winters or early spring periods in the Baltic Sea region within the decadal NAO-related climate variability (Ruprecht *et al.*, 2002) and a long-term, warming-related trend (Zhang *et al.*, 2007).

As a consequence, the analysis of the experimental data was refined by depicting the mesocosm system in a dynamic simulation model which was originally developed to analyze the factors driving the spring phytoplankton dynamics in large, deep Lake Constance (Tirok & Gaedke, 2007) and subsequently adapted to the specific conditions in the mesocosms. It is based on

ordinary differential equations, driven by time-series of water temperature and irradiance, and distinguishes between edible and less edible phytoplankton. The model was used to systematically disentangle the individual effects of altered temperature, light, grazing, and initial biomasses and plankton compositions. In particular, we address the role of indirect biotic effects in modifying the response of phytoplankton to climate change based on the hypothesis that trophic interactions may overrule direct climate effects, e.g. by a grazer-mediated inverse temperature effect.

Material and methods

Eight indoor mesocosms (1400 L, 1 m depth) filled with natural late winter plankton communities from Kiel Fjord, Western Baltic Sea, Germany, were run under four different temperature regimes (two parallels) from February to May 2005, 2006 and 2007. We intended to add mesozooplankton, mainly consisting of the copepods *Pseudocalanus* spp., *Paracalanus* spp., and *Oithona similis*, from net catches at long-term mean overwintering concentrations (Behrends, 1996). However, due to the strong interannual variation in zooplankton density and the limited possibility to homogenize zooplankton samples before inoculating the mesocosms, the realized start biomasses varied both interannual and between mesocosm from 54 to 104 $\mu\text{g L}^{-1}$ in 2005 (mean 82, SD 18), 7 to 33 $\mu\text{g L}^{-1}$ in 2006 (mean 25, SD 8) and 3 to 14 $\mu\text{g L}^{-1}$ in 2007 (mean 8, SD 4). This variability is lower than the interannual variability in the field (Behrends, 1996).

The mesocosms were gently mixed by a propeller to assure a homogeneous distribution of the plankton. Owing to technical reasons, the starting dates of the experiments differed somewhat between the years, but

the temperature and the light program were adjusted to a theoretical start on 4 February (Julian day 35). Water temperatures in the mesocosms reached the experimental temperatures within maximally 2–3 days, depending on the difference between *in situ* and experimental temperatures (maximally 6 °C, warmest treatment 2005 and ca. 4 °C in 2006 and 2007). The initial phytoplankton decline in 2005 cannot be attributed to a heat shock, because 2 and 4 °C warming relative to *in situ* temperatures did not lead to any initial decline in 2006, while there was an initial decline at all temperature treatments in 2005.

The temperatures followed the observed seasonal course of Kiel Bight, the coldest one ('baseline') corresponding to the decadal average 1993–2002 and the three others with +2, +4 and +6 °C temperature elevation above the baseline until the end of February. After that, the temperature difference between the treatments was reduced by 0.25 °C per month in order to mimic the less pronounced warming later in the year (Fig. 1a). For the sake of brevity, the initial temperature difference will be used to characterize the temperature treatments throughout this article.

The day-length, light intensity, and diel light pattern were identical for all mesocosms during each year. The day-length was adjusted to natural conditions. The natural solar irradiance (I_0) was calculated from astronomic models for each day (Brock, 1981) and reduced to 16% in 2005, 32% in 2007, and 64% in 2006 to mimic differences in cloudiness and underwater light attenuation. While each temperature regime was run in duplicate in each year, only one light regime could be run per year (for details see Sommer *et al.*, 2007; Sommer & Lengfellner, 2008). Hence, differences in light were confounded with the differences in initial phyto- and zooplankton biomasses and compositions.

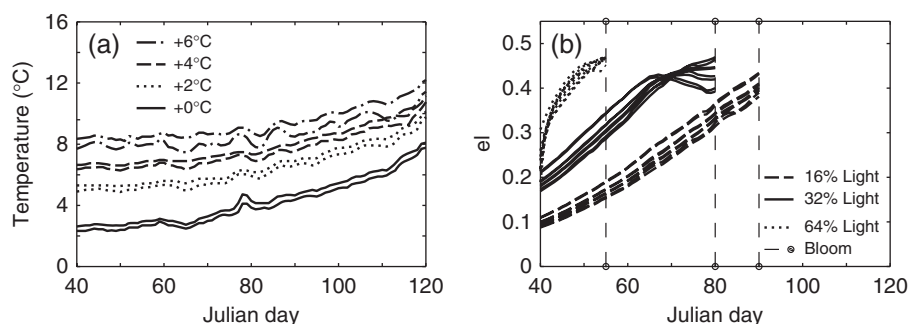


Fig. 1 (a) Temperature in the eight mesocosms (measured during the low light experiment and representative for all years) and (b) light regulation factor of primary production *el* in 2005 (lower group of lines, 16% irradiance), 2006 (upper group of lines, 64% irradiance) and 2007 (intermediate group of lines, 32% irradiance). *el* describes the extent by which the maximal primary production is reduced due to light limitation and depends on irradiance, temperature and self shading [cf. Eqn (A8)]. As self-shading depends on the simulated algal biomasses, results are only displayed until nutrient depletion and wall growth gained importance which is indicated by vertical lines.

Sampling and analysis

Phytoplankton was sampled three times per week from mid-depth (0.5 m) of the well-mixed mesocosms. Phytoplankton $>5\mu\text{m}$ were counted by inverted microscopy and distinguished at the genus level in most cases. Small phytoplankton were counted by a flow cytometer (FACScalibur, Becton Dickinson, San Jose, CA, USA) and distinguished by size and fluorescence of chlorophyll *a* and phycoerythrin. Phytoplankton biomass was estimated as carbon calculated from cell volumes (Menden-Deuer & Lessard, 2000) which was derived from linear measurements after approximation to the nearest geometric standard solid (for details see Sommer *et al.*, 2007; Sommer & Lengfellner, 2008).

For ciliates, subsamples of 100 mL were counted using a sedimentation chamber. Cell densities were converted to biovolume using the geometric proxies by Hillebrand *et al.* (1999) and the carbon conversion factors given by Putt & Stoecker (1989) (for details see Aberle *et al.*, 2007). Mesozooplankton was counted with a binocular microscope. Adult copepods and copepodites but not the nauplii were distinguished by genus and other mesozooplankton were separated into larval types. In order to diminish the mesozooplankton populations as little as possible the sampling volume had to be restricted to three times 5 L per mesocosm per week at the cost of counting precision (for details see Sommer *et al.*, 2007). Sample volume was replaced by unfiltered water from the Kiel Fjord, except for a short period during the medium light experiment in 2007 because of a bloom of the potentially harmful flagellate *Chattonella* sp. (Granéli & Hansen, 2006).

In the medium light experiment primary production measurements were performed using ^{14}C bicarbonate incubations (two replicates and one blank, incubated for 4–5 h). Subsequently, aliquots of 10 mL were filtered onto $0.2\mu\text{m}$ cellulose nitrate filters, fumed with 37% HCl fumes, and measured in 4 mL of Scintillation cocktail. Calculated daily primary production was corrected for actual light received during the incubation period (for details see Hoppe *et al.*, 2008).

Samples for the determination of particulate organic carbon (POC), nitrogen (PON) and phosphorus (POP) were taken one to three times per week. For this purpose, 50–500 mL of sample were filtered onto pre-combusted (5 h, 450°C) glass fiber filters (GF/F, Whatman, Maidstone, Kent, UK) and stored at -20°C . The filters for POC and PON were dried at 60°C for 6 h before analysis and measured on an elemental analyzer (EuroVector EA, Milan, Italy) after Sharp (1974). POP was determined colorimetrically after oxidation with potassium peroxodisulphate as described by Hansen & Koroleff (1999).

Model description

We adapted a dynamic simulation model which successfully reproduced the major patterns in the spring phytoplankton dynamics in large, deep Lake Constance (Tirok & Gaedke, 2007), to the specific conditions in the mesocosms. It was driven by time-series of water temperature and irradiance, and incorporated the state variables edible and less edible phytoplankton which differed only in their parametrization. Based on the feeding preferences of the dominant grazers (large ciliates and copepods), phytoplankton was subdivided into edible (diatoms and filamentous species $>500\text{--}1000\mu\text{m}^3$ cell volume, except for armored dinoflagellates, *Coscinodiscus* spp., *Dictyocha speculum* and *Pseudonitzschia* spp.) and less edible forms (autotrophic picoplankton, nanoplankton $<500\text{--}1000\mu\text{m}^3$ cell volume) (Sommer *et al.*, 2005; Sommer & Sommer, 2006).

In contrast to Tirok & Gaedke (2007) we did not include vertical heterogeneity and mixing, sedimentation, and background turbidity into our model because they were considered as less relevant in the well mixed, shallow mesocosms during the part of the experiment considered in this study. The nonlinear dependence of primary production on temperature and light was described using a temperature (eT) and a light (eI) regulation factor [for details see Eqns (A3) and (A8)]. Improving the model by Tirok & Gaedke (2007), their combined effect was calculated by assuming that primary production increased independently of temperature linearly with irradiance up to a threshold value close to light saturated production (Tilzer *et al.*, 1986) which increased with temperature [Eqn (A11)] (Hawes, 1990). Hence, under strongly light limiting conditions primary production is assumed to be independent of temperature (light reaction dominates) whereas when approaching light saturation, photosynthesis becomes increasingly sensitive to temperature as the speed of enzymatic processes gains importance (dark reaction). Hence, the minimum of saturated irradiance is temperature dependent [Eqn (A11), at low temperature saturation is achieved at lower irradiance].

Both algal groups experienced independently a dynamic mortality rate representing grazing losses that depended in a nonlinear, density-dependent form on current and previous algal densities [i.e. the grazing pressure increased with a time-lag with increasing algal densities and vice versa; Eqn (A16)]. By these means, predator dynamics and, thus, their grazing pressure followed their prey with a time lag adjusted to the response time of the dominant grazers. This implies implicitly the assumption that algal concentrations remained below the incipient limiting level due to increasing grazer biomasses and nutrient depletion at

higher algal concentrations. Following Tirelli & Mayzaud (2005) this assumption holds true except for short periods around the biomass peaks. During parts of the experiments ciliates contributed substantially to the grazing pressure in the mesocosms (Aberle *et al.*, 2007 and unpublished data) and their prey spectra strongly overlapped with those of the dominant copepods. To test the reliability of the assumptions and parametrization of this mortality term, total grazing pressure was inferred from the weighted sum of ciliate and copepod biomass where ciliate biomass was multiplied by two and copepod biomass by 0.5 to account for the higher weight-specific ingestion rates of the smaller-sized ciliates (Peters, 1983; Tirok & Gaedke, 2006 and literature cited therein; de Castro & Gaedke, 2008). Furthermore, losses by basal and activity-dependent respiration and exudation were accounted for.

In standard model runs, the starting values of the grazing losses at the first day of the simulation were calculated based on the initial algal biomasses [i.e. $M = m \times A^a$, cf. Eqn (A16)]. Since the observed initial algal and grazer biomass and the ratio between them greatly differed among study years, we subsequently altered them separately in different model scenarios.

Parametrization. Based on a large body of empirical evidence (e.g. Tilzer *et al.*, 1986; for details see discussion), we assumed a stronger temperature-dependence of heterotrophic than of autotrophic processes (cf. Table A1). We used the same parameter values as Tirok & Gaedke (2007) for the minimum optimal light intensity, the coefficient of self-shading, the temperature-dependence of auto- and heterotrophic processes (except for grazing), and exudation. Given the large differences in size and taxonomy between the algae rated as edible or less edible for the dominant grazer in Lake Constance (small ciliates and filter feeding cladocerans preferring small algae) and in the mesocosms (large ciliates and raptorial feeding copepods preferring larger phytoplankton) we changed the maximum growth rate of edible algae from 2.9 to 2.2 and of less edible algae from 1.6 to 1.4 (Banse, 1982; Blasco *et al.*, 1982; Sommer, 1989; Maranon, 2008).

We assumed for both types of algae the same basal and activity respiration. Copepod and ciliate biomass and the taxonomic composition of the ciliates strongly differed between the low, medium and high light experiments with large ciliates prevailing in the low light experiment. This was reflected in the model by a more pronounced density-dependence of the grazing rate in the low light ($a = 0.6$) than in the medium and high light experiment [$a = 0.3$, cf. Eqn (A16)]. These parameter adjustments were made by visualizing the fit of the model to the data using the measurements of algal biomass in mesocosms 1, 5 and

7 in each year. Biomass measurements of the other mesocosms and all measurements of grazer biomass were available for model validation. Within comprehensive sensitivity analyses all calibrated parameters (cf. Table A1) except for the coefficient of self-shading as well as the constant describing the time delay in the response of the mortality to altered algal biomass were altered within their ecologically reasonable ranges to avoid reporting results which are sensitive to the inevitable uncertainties in the parametrization (for details see Wiegand, 2008). We started the simulations with the biomasses observed 5 days after filling of the mesocosms.

We neglected nutrients in our model since we focussed on the development of the phytoplankton spring bloom during which severe nutrient depletion did not occur according to measurements of the sestonic C:P and C:N ratios. At the height and after the phytoplankton bloom nutrient depletion was relevant (average molar ratio during and after the bloom POC:POP > 150:1 and POC:PON > 20:1) which was, however, difficult to model as wall growth increasingly influenced the nutrient budget in the low and medium light experiments (Sommer *et al.*, 2007; Sommer & Lengfellner, 2008; J. Wohlers unpublished data). Consequently, we consider here only the simulation results until the height of the phytoplankton bloom. The latter was reached around Julian day 90 and 80 in the low and medium light experiment respectively, and very early in the high light experiment (ca. Julian day 45) which also started with very high initial algal biomasses. Hence, the period of observation and the number of data points not affected by nutrient dynamics is very limited in the high light experiment and we focus on the low and medium light experiments which are also more representative for natural conditions.

Results

The temperature variability was considerably larger among mesocosms (maximally 6 °C) than in time (ca. 1 °C increase until the phytoplankton peak; Fig. 1a). In contrast, irradiance strongly increased throughout the experiment and the extent by which the maximal primary production was reduced due to light limitation declined considerably until the bloom (Fig. 1b). Light conditions differed slightly between mesocosms within individual years (i.e. light treatments) due to the impact of temperature and self-shading, and strongly among years due to the differences in incoming irradiance.

In all mesocosms, a typical temporal pattern of a spring bloom with a subsequent decline of phytoplankton biomass was found. In the low and medium light (16% and 32% of I_0) experiments, phytoplankton biomass either declined initially (16%, Fig. 2a, e) or the

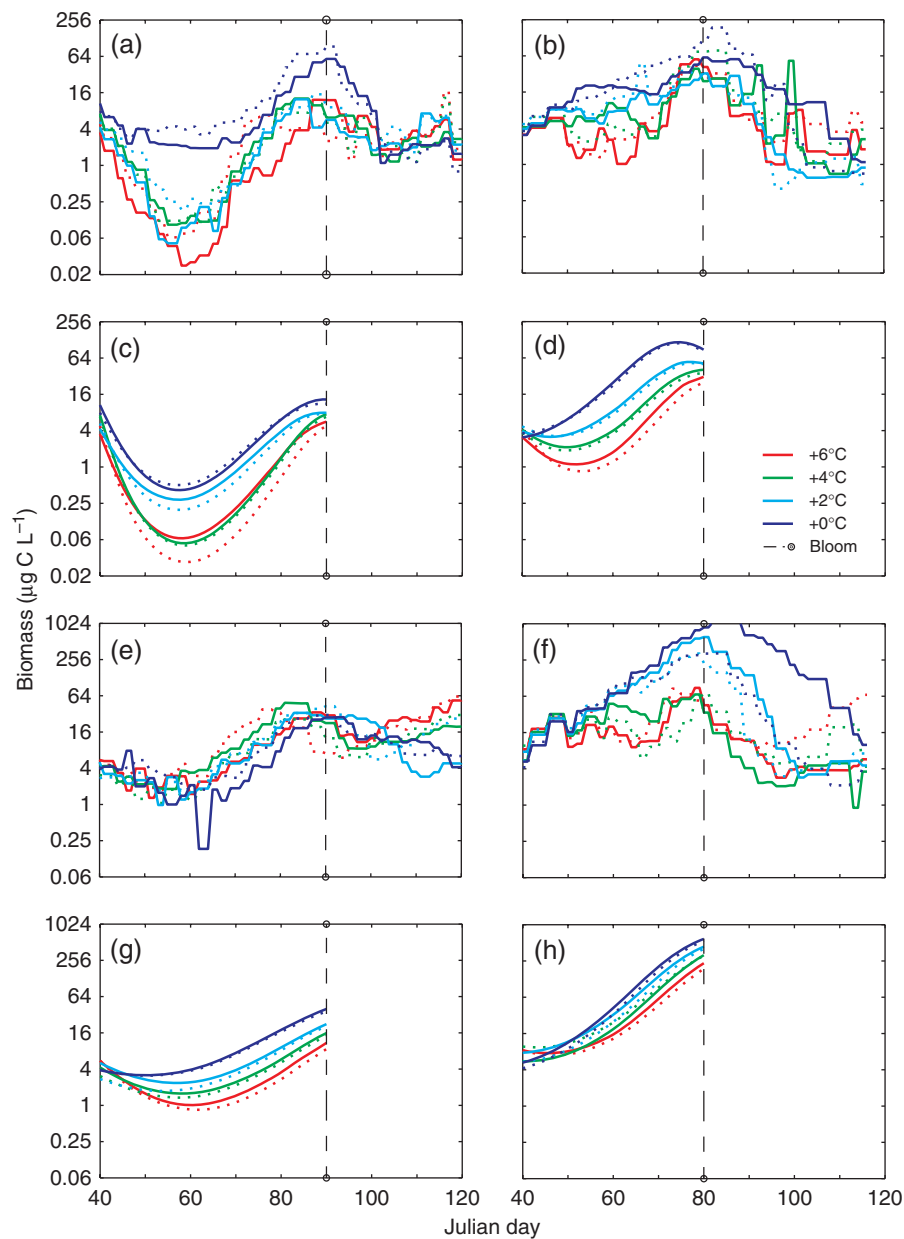


Fig. 2 Observed biomass of edible algae in (a) the low light ($16\% I_0$) and (b) the medium light ($32\% I_0$) experiment. Modelled biomass of edible algae in (c) the low light ($16\% I_0$) and (d) the medium light ($32\% I_0$) experiment. Observed biomass of less edible algae in (e) the low light ($16\% I_0$) and (f) the medium light ($32\% I_0$) experiment. Modelled biomass of less edible algae in (g) the low light ($16\% I_0$) and (h) the medium light ($32\% I_0$) experiment. Simulations were terminated after reaching peak algal biomasses when nutrient depletion and wall growth gained importance (i.e. Julian day 90 in the low light and day 80 in the medium light experiment).

initial positive net growth was temporally interrupted for a certain period of time (32%, Fig. 2b, f). The high light experiment started with an algal biomass already close to the peak value (cf. Fig. 4a, b). The observed dynamics of edible and less edible phytoplankton and their temperature-dependence differed strongly (Fig. 2a, b, e, f). Warm temperatures strongly enhanced the initial decline of edible phytoplankton after the onset of

the experiment under low and medium light conditions, whereas less edible algal biomass responded only weakly to temperature throughout the entire experiment (low light experiment, Fig. 2e) or temporally (medium light experiment, Fig. 2f). This is only explicable by a temperature-sensitive loss process largely restricted to edible algae (e.g. grazing) since primary production is limited by light.

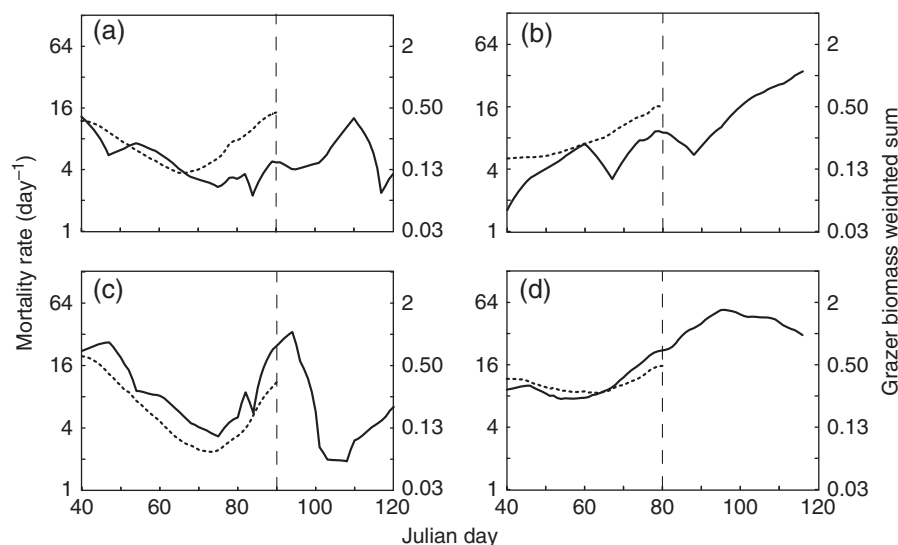


Fig. 3 Comparison between the observed surrogate for grazing pressure (full line, i.e. the weighted sum of ciliate and copepod biomass multiplied by the same temperature factor as used in the model) and the model derived grazing rate [dotted line, cf. Eqn (A16)]. (a) The coldest mesocosm at 16% irradiance, (b) the coldest mesocosm at 32% irradiance, (c) the warmest mesocosm at 16% irradiance, and (d) the warmest mesocosm at 32% irradiance. Simulations were terminated shortly after phytoplankton reaching peak biomasses when nutrient depletion and wall growth became important.

The model successfully reproduced the above mentioned patterns in the dynamics of the edible algae in the low and medium light experiments when using the observed temperature and light conditions and a strongly temperature-dependent grazing term ($Q_{10Hm} = 4$) (Fig. 2c, d). Considering details, modelled dynamics were somewhat faster than the observed ones in the medium light experiment, particularly in the cold mesocosms. During the initial part of the high light experiment, modelled biomasses of edible algae declined immediately in contrast to the observed ones which was mostly attributable to the differences in grazing pressure between the experiments and the model (for details see 'Discussion'). The simulated biomasses of less edible phytoplankton were quantitatively reasonable for the low light experiment, and for the cold treatments of the medium light experiment but too high for the warm ones (Fig. 2g, h). In addition, in the low light experiment, the observed biomass tended to increase first in the warmer and then in the colder mesocosms whereas it was the other way round in the simulations.

The modelled rate of specific net primary production started with values around 0.05 and 0.12 at the onset of the low and medium light experiment, respectively, and increased with increasing light availability up to 0.30 and 0.35 at the time of the bloom. They fell into the range of values observed during the first part of the medium light experiment. The dynamics of the grazing rates estimated by the model coincided in a remarkable

way with the summed grazer biomass for almost all mesocosms (Fig. 3).

Overall, the rather simple model successfully reproduced the major patterns observed in time and across temperature and light treatments for the edible fraction of the phytoplankton until nutrient depletion and wall growth became relevant. Dynamics of less edible algae were less well described by the model in several treatments. Hence, the model will not be used to analyze the potential impact of individual forcing factors on the less edible algae which are, however, of minor importance for the grazers focussed on during our study (large-sized ciliates and copepods).

To better understand the potential impacts of grazing-induced mortality and of climatic factors, we first tested the reaction of the edible algae to altered descriptions of grazing losses and to altered dynamics in the forcing factors. The model could not reproduce the observations when omitting the density-dependence or the temperature-dependence of the grazing term. The density-dependence was essential to reproduce the temporal dynamics in algal biomass and the temperature-dependence was essential to reproduce the pronounced differences in algal development among the different temperature treatments during the first part of the experiments. Replacing the observed strong increase in irradiance during the experiments (Fig. 1b) by the mean light intensity from days 35 to 90 ($3.4 \text{ W m}^{-2} \text{ day}^{-1}$ in the low light experiment) had a major impact on the model outcome. It resulted in a less pronounced decrease of the edible algae during the first

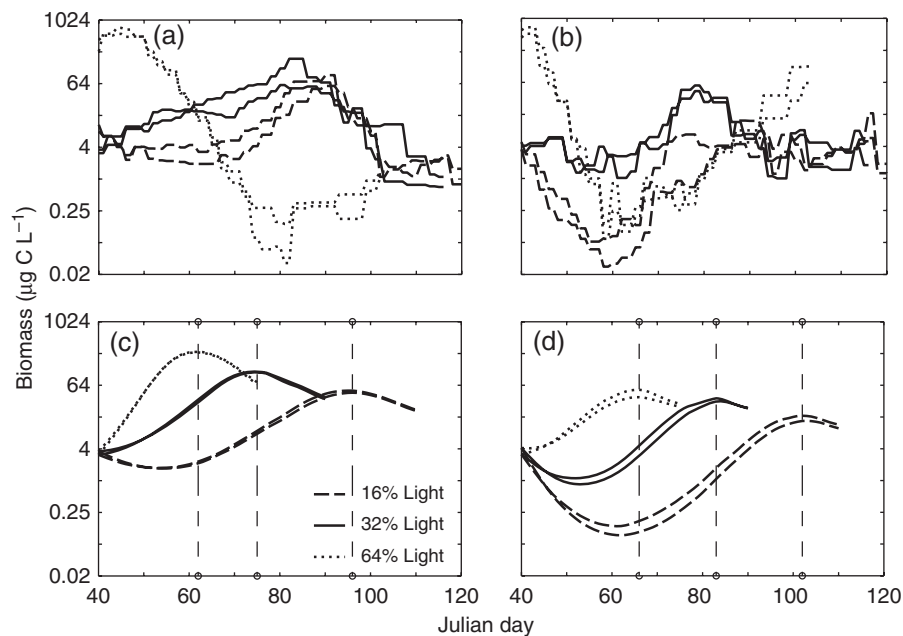


Fig. 4 Comparison between observed and modelled biomasses of edible algae. (a) observed biomasses of edible algae at low (---dashed line), medium (full line) and high light intensity (... dotted line) at the two cold temperature treatments (+ 0 °C), and (b) at the two warm temperature treatments (+ 6 °C). The different light treatments started with different initial phyto- and zooplankton biomasses. (c) Modelled biomass of edible algae at low (---dashed line), medium (full line) and high light intensity (... dotted line) at the two cold temperature treatments (+ 0 °C), and (d) at the warm temperature treatments (+ 6 °C) using the observed initial algal and grazer biomasses of the medium light experiment for all model runs. Simulations were terminated shortly after phytoplankton reaching peak biomasses.

part of the low light experiment and a subsequent lack of a distinct spring bloom.

Keeping the temperature constant at the initial value of the warmest mesocosms (8 °C) hardly reduced the goodness-of-fit of the simulations for the warmest mesocosms but led to unrealistic patterns in the cold ones. Vice versa, keeping the temperature constant at the initial value of the coldest mesocosms (2 °C) yielded good model fits for the coldest but very poor ones for the warmest mesocosms.

To separate the individual effects of light intensity, temperature, and initial algal and grazer biomasses which were partly confounded in the experiments, we modified one of these potentially influential factors at a time while keeping the others constant in the model. First, we compared the dynamics of the edible algae at low (16% I_0), medium (32% I_0) and high (64% I_0) light intensities at the four different temperature treatments using the same initial algal and grazer biomasses for all model runs (Fig. 4). In conjunction with temperature, the light intensity strongly affected the initial decline, and the timing and height of the algal spring bloom. The initial decline and the retarding of the bloom were strongest under low light and warm temperature conditions and vice versa. Furthermore, predicted peak values of algal biomass were lower at warmer temperatures since at a given light

intensity and, thus, specific primary production, losses balanced production already at a lower algal biomass at warmer temperatures due to the density- and temperature-dependence of the modelled grazing rate. The general pattern predicted by the model of retarding the bloom by low light, and a pronouncement of the initial decrease and a reduction of peak biomass by warmer temperatures was also found in the experiments starting with different initial biomasses (Fig. 4a, b).

The initial biomasses of edible algae were similar in the low and medium light experiment and approximately two orders of magnitude higher in the high light experiment (Fig. 4a, b). Because of operational limitations, the initial weighted and temperature-corrected grazer biomasses (ciliates and copepods) indicating the grazing pressure were two to three times higher in the low light (average 31 mg C m⁻³) than in the medium (10 mg C m⁻³) and high light (13 mg C m⁻³) experiment (Fig. 3). Furthermore, in the low light experiments copepods initially strongly dominated but declined throughout the experiment yielding subsequently an important role of ciliates, whereas in the medium light experiment ciliates contributed initially approximately an equal share but copepod biomass increased thereafter. As a consequence, the different light treatments which were run during different years, strongly de-

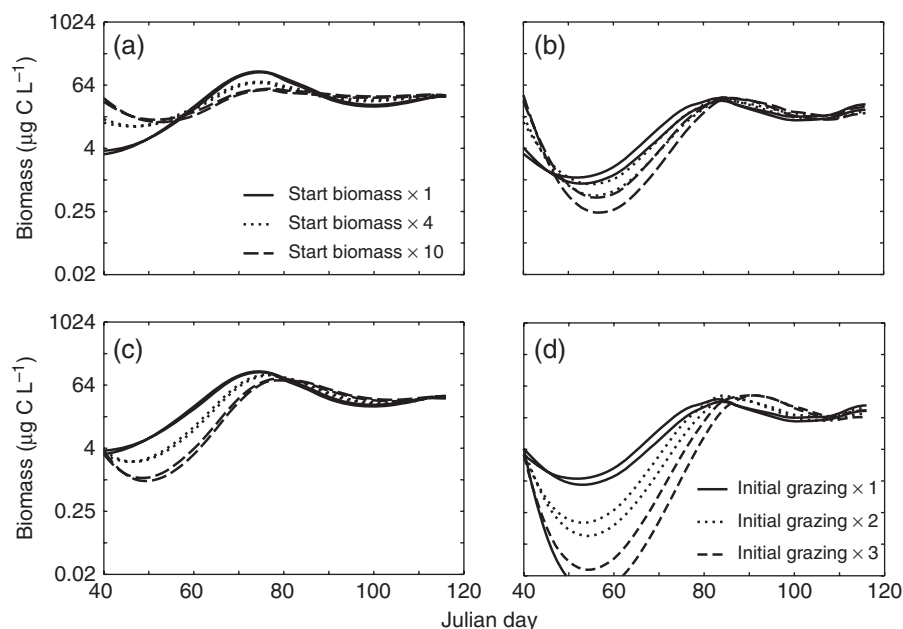


Fig. 5 Impact of the initial edible algal biomass (a, b), and of the initial grazing pressure (c, d) on edible spring phytoplankton dynamics at the two cold (a, c) and the two warm temperature treatments (b, d). Based on the observed interannual variability, the initial algal biomass was enhanced by a factor of 4 and 10 and the initial grazing pressure by a factor of 2 and 3 compared with the (low) one in the medium light experiment. Other conditions and starting values as in the medium light experiment.

viated in respect to the initial biomasses as well as the ratios between phytoplankton and grazers (and grazer composition).

Comparing model runs with different initial phytoplankton or grazer biomasses suggested that the initial conditions were memorized for several weeks and accounting for these differences improved the fit of the model to the data, in particular for the high light experiment. High initial phytoplankton biomasses did not result in an earlier or more pronounced peak due to the density dependently enhanced losses, particularly at warm temperatures under otherwise unchanged conditions (Fig. 5a, b). The initial grazing pressure strongly influenced algal dynamics during the first half of the experiment, in particular in the warmer treatments (Fig. 5c, d). A high initial grazing pressure comparable to that observed in the low light treatment led to a more or less pronounced decline of algal biomass also at medium light intensities. Similarly, the low initial grazing pressure which prevailed in the high light experiment, led to a more or less immediate increase of algal biomass also at medium light intensities especially at colder temperatures. This strongly suggests that the large differences in algal dynamics between the low and higher light experiments are not solely attributable to the differences in light conditions but also to the confounded effect of altered grazing pressure. As expected, the impact of the initial grazing intensity increased with temperature (Fig. 5).

Discussion

Model performance

The rather simple model reproduced reasonably well the temporal patterns of edible algae observed under different temperature and low and medium light conditions. In addition, observations and model results qualitatively agreed with respect to the extent of the initial phytoplankton decline and the retarding of the algal bloom by low light. A quantitative agreement is not to be expected as the initial biomasses differed among the experiments. This suggests that our model apparently considered the relevant processes correctly which determined the spring dynamics of edible algae until wall growth and nutrient depletion prevailed.

The high light experiment started with unusually high algal and low grazer biomasses and mimicked a light intensity well above natural conditions. This led to an extremely early algal bloom and onset of strong nutrient depletion which restricted the applicability of our model to a short period of time. It better reproduced the dynamics of the edible algae when accounting for the initially low grazing pressure. During the medium light experiment, observed phytoplankton biomasses declined unexpectedly shortly after an initial growth pulse. This cannot be explained by changes in grazer abundances which rather declined as well and were not reflected by the model. A tentative explanation is that

the replacement of the sample volume by water from the Kiel Fjord was stopped too late to prevent adverse allelopathic effects of the concurrent *Chattonella*-bloom in the Kiel Fjord (Granéli & Hansen, 2006).

Our model which was originally designed to predict spring algal dynamics in a large, deep lake, proved to be suitable to reproduce the development of edible algae in marine mesocosms under different temperature and light conditions after few modifications. This suggests that it may be valid for other pelagic systems as well where nutrient depletion is unimportant before the algal bloom. This further indicates that similar principal processes may regulate the onset of the spring bloom of edible phytoplankton in limnetic and marine temperate pelagic systems despite large differences e.g. in species composition.

As in Lake Constance, dynamics of less-edible algae were less well reflected by the model accounting for temperature, light, and grazing by copepods and ciliates. This suggests that for this functional algal group other influential factors exist which demand further identification. The subdivision into edible and less edible phytoplankton was based on the feeding preferences of copepods and larger ciliates and can only roughly approximate the gradual transition between highly edible and inedible algae and the fact that feeding preferences are species-specific and may temporally change depending on food availability. Copepods prefer larger protists ($>500\mu\text{m}^3$; Sommer *et al.*, 2005; Sommer & Sommer, 2006, and references therein), except for strongly armored dinoflagellates (not relevant in our study) and extremely large phytoplankton like *Coscinodiscus*. In addition to a rather general size preference, there are species-specific differences between a preference for immotile and for motile prey (Tiselius & Jonsson, 1990), the former leading to a preference for diatoms and the latter to a preference for ciliates and flagellates. In the overwintering copepod assemblage (mainly *Pseudocalanus* spp., *Paracalanus* spp., and *Oithona similis*) both feeding types were represented. Ciliates have frequently been reported to feed on smaller food items than the copepods (e.g. Sommer *et al.*, 2005), but the grazing experiments within the mesocosms indicated a strong overlap of ciliate and copepod food spectra (Aberle *et al.*, 2007). Therefore, we consider it justified to use one common category of 'edible algae' in our model.

The algae classified as less edible form a heterogeneous group consisting of algae smaller and larger than the edible ones and some species of the same size range which possess defending mechanisms. Phytoplankton classified as less edible in our mesocosms due to their small size may be substantially grazed by heterotrophic flagellates for which we have no data available. This point of view is supported by the observed temperature-sensitive retarding of growth and reduction of peak height in the medium but not in the low light

experiment. The heterogeneity within the group of less edible algae implies large differences in growth and loss rates which renders the fixed parameter values used in the model a coarse approximation given the pronounced changes in species composition (Sommer & Lengfellner, 2008). This might be improved by considering the very small and large species as well as those that show defending mechanisms separately when data on heterotrophic flagellates become available. Deviations between the observed and modelled biomasses of the less edible algae may imply inaccurate estimates of the self-shading in the model which in turn may influence the goodness-of-fit of the edible algae. This process became relevant in the medium light experiment at high algal biomasses.

Identification of four influential factors

Previously, most studies focussed on the direct and indirect effect of temperature on spring phytoplankton growth (e.g. Straile & Adrian, 2000) and more recently, others emphasized the (additional) importance of light (Siegel *et al.*, 2002; Peeters *et al.*, 2007; Tirok & Gaedke, 2007; Sommer & Lengfellner, 2008). We identified four factors which influenced the spring dynamics of edible phytoplankton: temperature (mostly via grazing pressure), light (cloudiness), grazing, and the initial phyto- and zooplankton biomass and composition.

(a) *Temperature*: The correct reflection of the measured mean absolute temperature in the model was essential to reproduce the differences in algal dynamics among mesocosms with the model whereas the temporal changes in temperature were not. The pronounced temperature-sensitivity during the first part of the experiments observed in the population development of the edible algae could only be reproduced by the model when assuming a very strong temperature-dependency of the grazing term (Q_{10} of 4 or 5) as at warmer temperatures, higher light intensities are required to offset the higher grazing losses and vice versa. Grazing activity, and in particular that of copepods which dominated the grazer biomass, is known to be strongly temperature-dependent but typically Q_{10} values lower than 4–5 were reported (e.g. zooplankton respiration: 1.8–3.0 (Ivleva, 1980; Ikeda *et al.*, 2001), zooplankton filtration rates: 2–3 (Prosser, 1973)). However, Isla *et al.* (2008) used *Pseudocalanus* spp. from the high light experiment and established a temperature-dependence of respiration rates which resulted in a Q_{10} -value of around 6.5 for the temperature range relevant in this study. Furthermore, the initial slope of the functional response curves (ingestion rate vs. food concentration) varied by a factor of 2.75 within a temperature interval of 6 °C, which extends to a Q_{10} -value of 5.4.

The enhanced grazing at higher temperature has the counterintuitive effect that algal biomasses initially decline more strongly than at cold temperatures which results in delayed and less expressed peaks (cf. Fig. 5c and d). The decrease of phytoplankton biomass with increasing temperatures concurs with similar predictions in the literature, but for different reasons. We identified grazing as the primary mechanism reducing biomass at higher temperatures, while for stratified ocean regions an enhanced thermal stratification and, therefore, less nutrient transport to the surface layer were considered decisive (Behrenfeld *et al.*, 2006). Another process enhancing the reduction of algal biomass at higher temperature are the higher respiratory losses which cannot be compensated by enhanced primary production under light limited conditions. This results in a decrease of net production with increasing temperature sustaining less organisms at higher trophic levels which, in turn, have higher weight-specific respiration losses themselves.

(b) *Light*: During the mesocosm experiments the seasonal increase in temperature was too slow to explain the rather sudden onset of phytoplankton net growth especially as it was counteracted by enhanced grazing at higher temperature. In contrast, light intensity changed pronouncedly during the study period. Overall, considering the temporal change in irradiance was essential to reproduce the observed biomass patterns with the model and the onset of the algal bloom depended on the increasing light intensity in spring. This is a major difference to water bodies with deep winter circulation. Here, the onset of thermal stratification or the cessation of wind-driven deep mixing during calm periods acts as a sudden switch, transforming the steep but gradual light increase into a step function. Nevertheless, mixed water column mean light intensities needed for the initiation of the spring net growth of algae are similar between the deep North Atlantic Ocean (Siegel *et al.*, 2002) and our mesocosms (Sommer & Lengfellner, 2008) which were intended to mimic shallow systems. Both studies suggested that phytoplankton net growth starts at a daily light dose of $1.3 \text{ mol photons m}^{-2} \text{ day}^{-1}$ on average (range: 0.96–1.75) independent of temperature. In contrast, the model predicted that the light intensity enabling the onset of net growth of edible algae should be temperature-dependent via the temperature-sensitive grazing intensity and, to a lesser extent, via temperature-sensitive respiratory losses. This may have passed unnoticed so far in the above mentioned studies considering larger scales implying heterogeneity also in the grazing pressure, and the entire phytoplankton which may be dominated by less edible forms. We suggest to repeat the analyses of the empirical data separately for various phytoplankton groups which differ in their susceptibility to different grazers.

(c) *Grazing*: Grazing was identified as a major factor influencing spring growth of edible phytoplankton unless their biomass was very low due to abiotic constraints. This was also found for large deep Lake Constance (Peeters *et al.*, 2007; Tirok & Gaedke, 2007) and is in line with Siegel *et al.* (2002) who argued, that the light threshold required to observe net algal growth is about twice as high as the threshold expected from phytoplankton physiological requirements alone. They explained this discrepancy by the need to achieve a growth rate outweighing grazing losses. The observed weighted grazer biomass and the grazing mortality calculated in the model coincided well for the large range in grazer composition and grazer dynamics suggesting that the rather simple representation of grazing losses in the model was sufficient to capture the dominant dynamics. Under *in situ* conditions the coupling of algal biomass and grazing losses may be reduced by a top-down control of the herbivores by carnivores which were neither considered in the mesocosm experiments nor in our model.

(d) *Initial conditions*: Our model results indicated that the initial phytoplankton and grazer biomasses may play an important role for the phytoplankton development throughout spring and that processes predominating during the previous year are memorized for many weeks by the system via the concentration of overwintering plankters. This asks for more intensive investigations during winter which is the most understudied period in limnetic and marine field and experimental research.

Relevance of cardinal points and prediction of future changes: Our process-based model demonstrated the impact of different bottom-up and top-down effects on algal dynamics which suggests that the analysis of temporal cardinal points *sensu* Round (1973) (e.g. maxima and minima in the annual biomass curve or transitions in taxonomic composition) has a limited capacity to develop a mechanistic understanding of climate change impacts on plankton succession. An earlier peak may be caused both by an earlier attainment of the phytoplankton carrying capacity and/or by an earlier increase of loss rates (Thackeray *et al.*, 2008). Identifying the timing of cardinal points in the climate change literature (Stratle & Adrian, 2000 and other similar studies) was inspired by terrestrial vegetation phenology, e.g. the timing of the flowering of apples, which differ from plankton succession in two points: Firstly, they are only bottom-up not top-down controlled, and secondly they represent events within the life history of individuals while phytoplankton blooms are community level events which involve several species and generations and do not account for the composite nature of temporal cardinal points in phytoplankton seasonality.

In the light of an ongoing climate change increasing cloudiness and atmospheric water vapor content are predicted for Northern Europe (Ruprecht *et al.*, 2002;

Zhang *et al.*, 2007) and therefore our study aimed at analyzing the overall importance of the effect of cloud cover, a factor that has been neglected in the literature so far. Our study predicts that increasing cloudiness will retard phytoplankton net growth and reduce peak heights. Increasing winter and spring temperature is likely to exhibit complex indirect effects via changes in overwintering phytoplankton and grazer biomasses and ambient grazing pressure. It will presumably also affect the phytoplankton composition due to the differential susceptibility of algal species to different grazer types and calls for more intensive studies during late winter.

Up-scaling to field conditions: The combination of controlled mesocosm experiments and a process-driven model allowed to disentangle a complex interplay of abiotic and biotic factors and processes regulating spring phytoplankton growth which are inevitably confounded and superimposed by more noise in field data. The scale of the mesocosm experiments allowed to include all major plankton groups and the model does not rely on any assumptions specific to the mesocosms. Hence, up-scaling of our results to field conditions appears appropriate, e.g. by combining our biological model with a hydrodynamic model accounting for vertical stratification and/or horizontal mixing if this is relevant for the particular system under consideration.

Wider implications for other systems: Early examples of biological responses to global warming or periodic climate variability focused on single species or bulk biomass parameters in terrestrial systems, such as chlorophyll for autotrophs, while neglecting biotic interactions (Walther *et al.*, 2002 and citations therein). Typical responses included pole-ward and altitudinal extensions of geographic species ranges (also emphasized in Thuiller, 2007) and shifts in seasonal activity and growth patterns (e.g. Cleland *et al.*, 2007). Examples from the less-studied pelagic systems showed an advancement of the seasonal abundance patterns of phyto- and zooplankton with warming (Straile, 2000; Edwards *et al.*, 2002) and species replacements in zooplankton communities (Möllmann *et al.*, 2000; Hays *et al.*, 2005) and were related to climate variability within the well known North Atlantic Oscillation. However, unexpected exceptions emerged as well. Regarding the diatom spring bloom in the shallow Southern North Sea, either a retardation during recent warming (Wiltshire & Manly (2004) or no directional change, but (unexplained) large interannual variations in the timing of the spring bloom was found (Wiltshire *et al.*, 2008). Similarly, in Kiel Fjord the spring phytoplankton bloom seems to occur several weeks later after a mild than after a cold winter (U. Sommer, unpublished data). These exceptions to the 'the warmer-the earlier' rule have drawn the attention to the role of potentially confounding factors such as light and of biotic interactions.

In a grassland experiment analyzing the response to an altered precipitation regime biotic species interactions were found to strongly influence responses to changing climate overturning direct climatic effects (Suttle *et al.*, 2007). This is in line with the predominately grazer-mediated inverse temperature effect found in our pelagic study. It stresses the overall importance of studying not only the direct consequences of altered climate conditions to predict the consequences of climate change as they may be overruled by indirect ones mediated by species interactions and may lead to the opposite responses as expected. Species-mediated indirect effects have not yet been acknowledged in most studies related to climate change (Suttle *et al.*, 2007) but are of considerable importance for population dynamics in complex, multi-trophic food webs which represent the rule rather than the exception in both terrestrial as well as pelagic ecosystems. Thus, there is a strong need to consider not only direct but also indirect effects, often mediated by biotic interactions, when addressing climate change impacts on both terrestrial as well as aquatic ecosystems.

Acknowledgements

Maintenance of mesocosms, sampling, and microscopic counting were supported by Thomas Hansen and Horst Thomanetz. Francisco de Castro gave advice on computational issues. We thank two anonymous referees for their thoughtful and stimulating comments. Ulf Riebesell, Klaus Jürgens, and Hans-Georg Hoppe acted as PIs of the projects by which the co-authors Julia Wohlers and Petra Breithaupt were financed. M. R.-B., K. T., P. B., K. L. and J. W. received funding from the German Research Foundation (DFG) within the priority program 1162 'The impact of climate variability on aquatic ecosystems (AQUASHIFT)'.

References

- Aberle N, Lengfellner K, Sommer U (2007) Spring bloom succession, grazing impact and herbivory selectivity of ciliate communities in response to winter warming. *Oecologia*, **150**, 668–681.
- Banase K (1982) Cell volumes, maximal growth rates of unicellular algae and ciliates, and the role of ciliates in the marine pelagial. *Limnology and Oceanography*, **27**, 1059–1071.
- Baretta JW, Ebenhöf W, Ruardij P (1995) The European-Regional-Seas-Ecosystem-Model, a complex marine ecosystem model. *Netherlands Institute for Sea Research*, **33**, 233–246.
- Behrenfeld MJ, O'Malley RT, Siegel DA *et al.* (2006) Climate-driven trends in contemporary ocean productivity. *Nature*, **444**, 752–755.
- Behrends G (1996) Long-term investigation of seasonal zooplankton dynamics in Kiel Bight, Germany.: In: Proceedings of the 13th Symposium of Baltic and marine Biology, pp. 93–98.
- Blasco D, Packard TT, Garfield PC (1982) Size dependence of growth rate, respiratory electron transport system activity, and chemical composition of marine diatoms in the laboratory. *Journal of Phycology*, **18**, 58–63.

- Brock TD (1981) Calculating solar radiation for ecological models. *Ecological Modelling*, **14**, 1–19.
- Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to global change. *Trends in Ecology and Evolution*, **22**, 357–366.
- de Castro F, Gaedke U (2008) The metabolism of lake plankton does not support the metabolic theory of ecology. *Oikos*, **117**, 1218–1226.
- Edwards M, Beaugrand G, Reid PC, Rowden A, Jones MB (2002) Ocean climate anomalies and the ecology of the North Sea. *Marine Ecology Progress Series*, **239**, 1–10.
- Fransz HG, Colebrook JM, Gamble JC *et al.* (1991) The Zooplankton of the North-Sea. *Netherlands Journal of Sea-Research*, **28**, 1–52.
- Gaedke U, Hochstädtter S, Straile D (2002) Interplay between energy limitation and nutritional deficiency: empirical data and food web models. *Ecological Monography*, **72**, 251–270.
- Geider RJ (1992) Respiration: taxation without representation? In: *Primary Productivity and Biogeochemical Cycles in the Sea* (eds Falkowski PG, Woodhead AD), pp. 333–360. Plenum Press, New York.
- Gerten D, Adrian R (2001) Differences in the persistency of the North Atlantic Oscillation signal among lakes. *Limnology and Oceanography*, **46**, 448–455.
- Granéli E, Hansen PJ (2006) Allelopathy in harmful algae: a mechanism to compete for resources? In: *Ecology of Harmful Algae*. *Ecol Stud*, Vol. 189 (eds Granéli E, Turner JT), pp. 189–201. Springer, Berlin.
- Hancke K, Glud RN (2004) Temperature effects on respiration and photosynthesis in three diatom-dominated benthic communities. *Aquatic Microbial Ecology*, **37**, 265–281.
- Hansen HP, Koroleff F (1999) Determination of nutrients. In: *Methods of Seawater Analysis*, 3rd edn (eds Grasshoff K, Kremling K, Ehrhardt M), pp. 159–228. Wiley VCH, Weinheim.
- Häse C, Gaedke U, Seifried A, Beese B, Tilzer MM (1998) Phytoplankton response to re-oligotrophication in large and deep Lake Constance: photosynthetic rates and chlorophyll concentrations. *Archives of Hydrobiology Special Issues Advances in Limnology*, **53**, 159–178.
- Hawes I (1990) The effects of light and temperature on photosynthate partitioning in Antarctic freshwater phytoplankton. *Journal of Plankton Research*, **12**, 513–518.
- Hays GC, Richardson AJ, Robinson C (2005) Climate change and marine plankton. *Trends in Ecology and Evolution*, **20**, 337–344.
- Hillebrand H, Dürselen CD, Kitschel D, Pollinger U (1999) Biovolume calculations for pelagic and benthic microalgae. *Journal of Phycology*, **35**, 403–424.
- Hoppe HG, Breithaupt P, Walther K, Koppe R, Bleck S, Sommer U, Jürgens J (2008) Climate warming in winter affects the coupling between phytoplankton and bacteria during the spring bloom: a mesocosm study. *Aquatic Microbial Ecology*, **51**, 105–115.
- Ikeda T, Kanno Y, Ozaki K, Shinada A (2001) Metabolic rate of epipelagic copepods as a function of body mass and temperature. *Marine Biology*, **139**, 587–596.
- IPCC (International Panel on Climate Change) (2007) *Climate Change 2007: The Physical Science Basis. In: Contribution of Working Group I to Fourth Assessment Report of the Intergovernmental Panel on Climatic Change* (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB *et al.*), 996 pp. Cambridge, United Kingdom and New York, NY, USA.
- Isla A, Lengfellner K, Sommer U (2008) Physiological response of the copepod *Pseudocalanus* sp. in the Baltic Sea at different thermal scenarios. *Global Change Biology*, **14**, 895–906.
- Ivleva IV (1980) The dependence of crustacean respiration rate on body mass and habitat temperature. *Internationale Revue der Gesamten Hydrobiologie*, **65**, 1–47.
- Kotzur S (2003) *Ein pelagisches Ökosystem-Modell zur Analyse von Mesokosmos-Experimenten*. Thesis, University of Oldenburg, 98 pp.
- Maranon E (2008) Interspecific scaling of phytoplankton and cell-size in the field. *Journal of Plankton Research*, **30**, 157–163.
- Menden-Deuer S, Lessard EJ (2000) Carbon to volume relationships for dinoflagellates, diatoms, and of the protist plankton. *Limnology and Oceanography*, **45**, 569–579.
- Möllmann C, Kornilovs G, Sidrevics L (2000) Long-term dynamics of main mesozooplankton species in the central Baltic Sea. *Journal of Plankton Research*, **22**, 2015–2038.
- Peeters F, Straile D, Lorke A, Ollinger D (2007) Turbulent mixing and phytoplankton spring bloom development in a deep lake. *Limnology and Oceanography*, **52**, 286–298.
- Peters RH (ed.) (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge, MA.
- Prosser CL (1973) *Comparative Animal Physiology*. Saunders, London.
- Putt M, Stoecker DK (1989) An experimentally determined carbon: volume ratio for marine “oligotrichous” ciliates from estuarine and coastal waters. *Limnology and Oceanography*, **34**, 1097–1103.
- Riley GA (1957) Phytoplankton of the North Central Sargasso Sea. *Limnology and Oceanography*, **2**, 252–270.
- Rose JM, Caron DA (2007) Does low temperature constrain the growth rates of heterotrophic protists? Evidence and implications for algal blooms in cold waters. *Limnology and Oceanography*, **52**, 886–895.
- Round FE (1973) The growth and succession of algal populations in fresh waters. *Mitteilungen der Internationalen Vereinigung für Limnologie*, **19**, 70–99.
- Ruprecht E, Schröder SS, Uhl S (2002) On the relation between NAO and water vapour transport towards Europe. *Meteorologische Zeitschrift*, **11**, 395–401.
- Sharp JH (1974) Improved analysis for particulate organic carbon and nitrogen from seawater. *Limnology and Oceanography*, **19**, 984–989.
- Siegel DA, Doney SC, Yoder JA (2002) The North Atlantic spring phytoplankton bloom and Sverdrup’s critical depth hypothesis. *Science*, **296**, 730–733.
- Sommer U (1989) Maximal growth rates of Antarctic phytoplankton: only weak dependence on cell size. *Limnology and Oceanography*, **34**, 1109–1112.
- Sommer U, Aberle N, Engel A *et al.* (2007) An indoor mesocosm system to study the effect of climate change on the late winter and spring succession of Baltic Sea phyto- and zooplankton. *Oecologia*, **150**, 655–667.
- Sommer U, Hansen T, Blum O, Holzner N, Vadstein O, Stibor H (2005) Copepod and microzooplankton grazing in mesocosms fertilised with different Si:N ratios: no overlap between food spectra and Si:N influence on zooplankton trophic level. *Oecologia*, **142**, 274–283.

- Sommer U, Lengfellner K (2008) Climate change and the timing, magnitude and composition of the phytoplankton spring bloom. *Global Change Biology*, **14**, 1199–1208.
- Sommer U, Sommer F (2006) Cladocerans versus copepods: the cause of contrasting top-down controls in freshwater and marine phytoplankton. *Oecologia*, **147**, 183–194.
- Steele JH (1962) Environmental control of photosynthesis in the sea. *Limnology and Oceanography*, **7**, 137–150.
- Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan KS, Lima M (2002) Ecological effects of climate fluctuations. *Science*, **297**, 1292–1296.
- Straile D (2000) Meteorological forcing of plankton dynamics in a large and deep continental European lake. *Oecologia*, **122**, 44–50.
- Straile D, Adrian R (2000) The North Atlantic Oscillation and plankton dynamics in two European lakes – two variations on a general theme. *Global Change Biology*, **6**, 663–670.
- Suttle KB, Thomsen MA, Power ME (2007) Species interactions reverse grassland responses to changing climate. *Science*, **315**, 640–642.
- Sverdrup HU (1953) On conditions for the vernal blooming of phytoplankton. *Journal du Conseil International pour l'Exploration de la Mer*, **18**, 287–295.
- Thackeray SJ, Jones ID, Maberly SC (2008) Long-term change in the phenology of spring phytoplankton: species-specific responses to nutrient enrichment and climatic change. *Journal of Ecology*, **96**, 523–535.
- Thuiller W (2007) Climate change and the ecologist. *Nature*, **448**, 550–542.
- Tilzer MM, Elbrächter M, Gieskes W, Beese B (1986) Light-temperature interactions in the control of photosynthesis in Antarctic phytoplankton. *Polar Biology*, **5**, 105–111.
- Tirelli V, Mayzaud P (2005) Relationship between functional response and gut transit time in the calanoid copepod *Acartia clausi*: role of food quantity and quality. *Journal of Plankton Research*, **27**, 557–568.
- Tirok K, Gaedke U (2006) Spring weather determines the relative importance of ciliates, rotifers and crustaceans for the initiation of the clear-water phase in a large, deep lake. *Journal of Plankton Research*, **28**, 361–373.
- Tirok K, Gaedke U (2007) The effect of irradiance, vertical mixing and temperature on spring phytoplankton dynamics under climate change: long-term observations and model analysis. *Oecologia*, **150**, 625–642.
- Tiselius P, Jonsson PR (1990) Foraging behaviour of six calanoid copepods: observations and hydrodynamic analysis. *Marine Ecology Progress Series*, **66**, 22–33.
- Turner JT, Borkman DG, Hunt CD (2006) Zooplankton of Massachusetts Bay, USA, 1992–2003: relationships between the copepod *Calanus finmarchicus* and the North Atlantic Oscillation. *Marine Ecology-Progress Series*, **311**, 115–124.
- Walther GR *et al.* (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Weyhenmeyer GA (2001) Warmer winters: are planktonic populations in Sweden's largest lake affected? *Ambio*, **30**, 565–571.
- Weyhenmeyer GA, Blenckner T, Pettersson K (1999) Changes of the plankton spring outburst related to the North Atlantic oscillation. *Limnology and Oceanography*, **44**, 1788–1792.
- Wiegand I (2008) *Prozessorientierte Modellierung der Reaktion des Phytoplanktons auf Veränderungen der Bewölkung und Temperatur im zeitigen Frühjahr*. Thesis, University Potsdam, 62 pp.
- Wiltshire KH, Malzahn AM, Wirtz K *et al.* (2008) Resilience of North Sea phytoplankton spring bloom dynamics: an analysis of long-term data at Helgoland Roads. *Limnology and Oceanography*, **53**, 1294–1302.
- Wiltshire KH, Manly BFJ (2004) The warming trend at Helgoland Roads, North Sea: phytoplankton response. *Helgoland Marine Research*, **58**, 269–273.
- Zhang X, Zwiers FW, Hegerl GC *et al.* (2007) Detection of human influence on twentieth-century precipitation trends. *Nature*, **448**, 461–448.

Appendix A

Model equations

Parameters are indicated by \sim , e.g. \tilde{r} . Their values are provided in Table A1. Variables taken from time series are indicated by (t) : water temperature ($^{\circ}\text{C}$) – $T(t)$, irradiance (W m^{-2}) – $Irr(t)$. The following indices were used:

i: *we*, *le*, *tot* referring to edible (*we*), less edible (*le*) and total phytoplankton (*tot*)

j: *A*, *H*, *M* referring to autotrophic (*A*), heterotrophic (*H*) and mortality (*M*) processes

Algal dynamics: A_i (mg C m^{-3}):

$$\frac{dA_i}{dt} = (prod_i - resa_i - exud_i - resb_i)A_i - M_i \cdot eT_M \cdot A_i, \quad (\text{A1})$$

$$\text{Production rate}(\text{day}^{-1}) : prod_i = \tilde{r}_i \cdot eT_A \cdot eI. \quad (\text{A2})$$

with temperature regulation factor:

$$eT_j = \tilde{Q}_{10,j}^{\frac{(T(t)-10)}{10}} \quad (\text{A3})$$

and light regulation factor eI (adopted from Baretta *et al.* (1995) and Kotzur (2003), for details see below). Primary production of algal group i per m^3 and day ($prod_i$), averaged over the water column, is calculated as

$$prod_i = \frac{1}{\tilde{d}} \int_0^{\tilde{d}} p_i(I(z)) dz \quad (\text{A4})$$

with $p_i(I(z))$: production at depth z of algal group i , $I(z)$: photosynthetic active irradiance at depth z , $I(z) = I(0)e^{-\kappa z}$ κ : vertical extinction coefficient (m^{-1})

Substitution results in : $prod_i$

$$= \frac{1}{\kappa \cdot \tilde{d}} \int_{I(\tilde{d})}^{I(0)} \frac{p_i(I)}{I} dI, \quad (\text{A5})$$

$p_i(I)$ was calculated following Steele (1962):

$$p_i(I) = \tilde{r}_i \frac{I}{I_{opt}} e^{\left(1 - \frac{I}{I_{opt}}\right)}. \quad (\text{A6})$$

The resulting function of the primary production is

$$prod_i = \frac{1}{\kappa \cdot \tilde{d}} \int_{I(\tilde{d})}^{I(0)} \frac{1}{I} \tilde{r}_i \frac{I}{I_{opt}} e^{\left(1 - \frac{I}{I_{opt}}\right)} dI. \quad (\text{A7})$$

Integration results in

$$prod_i = \tilde{r}_i \underbrace{\frac{1}{\kappa \cdot \tilde{d}} \left(e^{\left(1 - \frac{I(\tilde{d})}{I_{opt}}\right)} - e^{\left(1 - \frac{I(0)}{I_{opt}}\right)} \right)}_{eI}. \quad (A8)$$

Extinction coefficient:

$$\kappa = \tilde{selfsh} \cdot A_{tot}. \quad (A9)$$

Radiation integrated over the water column (W m^{-2}):

$$I_m = Irr \frac{(1 - e^{(-\kappa \tilde{d})})}{\kappa \cdot \tilde{d}}. \quad (A10)$$

Minimum of saturated irradiance:

$$I_{opt_min_t} = I_{opt_min} eT_A. \quad (A11)$$

Optimum irradiance (W m^{-2}):

$$I_{opt} = \max(I_m, I_{opt_min_t}). \quad (A12)$$

Activity-dependent respiration rate (day^{-1}):

$$resa_i = \tilde{pura} (prod_i - exud_i). \quad (A13)$$

Activity-dependent exudation rate (day^{-1}):

$$exud_i = \tilde{puea} \cdot prod_i. \quad (A14)$$

Basal respiration rate (day^{-1}):

$$resb_i = \tilde{srs}_i \cdot eT_H. \quad (A15)$$

Mortality rate (day^{-1}):

$$\frac{dM_i}{dt} = \frac{1}{\tilde{\tau}_i} (\tilde{m}_i \cdot A_i^a - M_i). \quad (A16)$$

Model parameters (Table A1)

Table A1 Full list of model parameters. we: edible algae, le: less edible algae

Parameter	Symbol	Value	Unit	Source
Depth of euphotic water layer	\tilde{d}	1	m	Depth of mesocosms
Minimal PAR of saturated photosynthesis	I_{opt_min}	40	W m^{-2}	Baretta <i>et al.</i> (1995), Kotzur (2003)
Self shading coefficient	\tilde{selfsh}	0.002	mg C m^{-2-1}	Calibrated and validated with primary production measurements of Lake Constance (Häse <i>et al.</i> , 1998)
Q_{10} value for autotrophic processes	$\tilde{Q}_{10,A}$	1.5	—	Stronger temperature-dependence of heterotrophic than of autotrophic processes (Hancke & Glud, 2004; Rose & Caron, 2007)
Q_{10} value for heterotrophic values	$\tilde{Q}_{10,H}$	2.0	—	
Q_{10} value for mortality representing grazing	$\tilde{Q}_{10,M}$	4.0	—	Calibrated, copepod grazing is highly sensitive to temperature (Isla <i>et al.</i> , 2008; for details see text)
Potential growth rate of edible algae at 10°C	\tilde{r}_{we}	2.2	day^{-1}	Calibrated with measurements of mesocosm 1, 5 and 7 in 2005 and lit. (see Materials and methods)
Potential growth rate of less edible algae at 10°C	\tilde{r}_{le}	1.4	day^{-1}	Calibrated with measurements of mesocosm 1, 5 and 7 in 2005 and lit. (see Materials and methods)
Activity exudation rate at 10°C	\tilde{puea}	0.1	day^{-1}	Baretta <i>et al.</i> (1995), Gaedke <i>et al.</i> (2002)
Activity respiration rate at 10°C	\tilde{pura}	0.25	day^{-1}	Geider (1992)
Basal respiration rate of edible algae at 10°C	\tilde{srs}_{we}	0.1	day^{-1}	Baretta <i>et al.</i> (1995), Gaedke <i>et al.</i> (2002)
Basal respiration rate of less edible algae at 10°C	\tilde{srs}_{le}	0.05	day^{-1}	Baretta <i>et al.</i> (1995), Gaedke <i>et al.</i> (2002)
Exponent for density dependent mortality	\tilde{a}	0.6 for 2005 0.3 for 2006 and 2007	—	Reflects the different grazer composition among years, calibrated with measurements of mesocosm 1, 5 and 7 in 2005, 2006, 2007
Time delay in density dependent mortality for edible and less edible algae	$\tilde{\tau}$	10	day	The response time is dominated by ciliates and nauplii
Mortality parameter of edible algae	\tilde{m}_{we}	0.3	day^{-1}	Calibrated with measurements of mesocosm 1, 5 and 7 in 2005
Mortality parameter of less edible algae	\tilde{m}_{le}	0.07	day^{-1}	Calibrated with measurements of mesocosm 1, 5 and 7 in 2005, 2006, 2007